



## FOSSIL BATS FROM MESOAMERICA <sup>1</sup>

(With 1 figure)

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**ABSTRACT:** Recent bats (Mammalia, Chiroptera) represent one of the most diverse mammalian orders, with more than 1,000 species, but the fossil record is poorly known. To date, records are for 41 species from 17 Mesoamerican localities in México (15) and Central America (2). This number corresponds to 24.8% of the 165 currently-known living bats for the region, pertaining to six out of eight known families. Most of the records are from Rancholabrean age deposits, with only one extinct species known for Pliocene sediments and two Pleistocene extinct vampire bat species. All other species presently range in the same region, but two of them. Most localities are cave deposits that correspond to the cave roosting habits for most of the species, either exclusive or temporal; only six are open spaces. Most of the fossils represent species that are insectivores (24), while others are frugivores (6), nectarivores (5), blood-eaters (4), and carnivores (2). The most dramatic change is with the blood-eater bats. While in the past there were three species within the genus *Desmodus*, only one is extant at present. Finally, future fieldwork should include the recovery of microremains from cave deposits to increase the findings of bats and other small vertebrates.

**Key Words:** Chiroptera. Fossils. Mesoamerica. Bats.

**RESUMEN:** Los murciélagos fósiles de Mesoamérica.

Los murciélagos (Mammalia, Chiroptera) conforman uno de los órdenes de mamíferos más diversos en el mundo, con más de 1,000 especies, pero no es el caso en el registro fósil por diversas razones. Hasta el momento, se han registrado 41 especies procedentes de 17 localidades fosilíferas mesoamericanas de México (15) y Centroamérica (2). Dicho número corresponde al 24.8% del total de especies que actualmente se conocen para la región (165) y representan a seis de las ocho familias de murciélagos registradas en la misma. La mayor parte de los registros corresponden a restos óseos procedentes de depósitos de Edad Rancholabreana; una sola especie ha sido registrada para el Plioceno, así como dos especies extintas de vampiros pleistocénicos. Las demás especies se distribuyen actualmente en la misma región de donde proceden los restos fósiles, con excepción de dos de ellas. La mayor parte de las localidades corresponden a cuevas y sólo seis son depósitos abiertos; lo mismo corresponde a los hábitos de reposo de las especies identificadas, la mayoría son cavernícolas exclusivas o eventuales. Con respecto a los gremios alimentarios representados, hay 24 murciélagos insectívoros, 6 frugívoros, 5 polinívoros, 4 sanguinívoros y 2 carnívoros. Lo más notorio es el registro de los sanguinívoros, el que ha cambiado de manera significativa, pues en el pasado se conocieron tres especies dentro del mismo género, *Desmodus*. Finalmente, es indispensable que las exploraciones en las cuevas sean planificadas de tal manera, que esto permita la recuperación y el estudio tanto de los mamíferos voladores como de otros vertebrados pequeños presentes en los depósitos.

**Palabras clave:** Chiroptera. Fósiles. Mesoamérica. Murciélagos.

### INTRODUCTION

Recent bats (Mammalia, Chiroptera) are one of the most diverse mammalian orders with more than 1,000 species. Such diversity should be found in the past, but the fossil record for these animals is very poorly known (TEELING *et al.*, 2005). In this report, fossil bats from Mesoamerica (México to Panamá) are documented, an area in which 165 bat species live at present (modified from HUTSON

*et al.*, 2001). Such species pertain to 8 families and 83 genera, with mixed affinities for Neartic and Neotropical regions.

### MATERIAL AND METHODS

Published reports have been reviewed and a regional map with the locality records was prepared. All the records are from deposits of Holocene or older age, mostly Pleistocene.

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## LOCALITIES

The known localities (Fig.1 - numbers correspond to the following list; Tab.1) are:

MÉXICO (modified from ARROYO-CABRALES & POLACO, 2003)

(1) Yepómera, Chihuahua

The deposit is near the town of Yepómera, at 1,500masl, in northern México. As one of the most important Pliocene localities in México, it contains the Hemphillian and Blancan faunas. All 37 mammal species known in the Yepómera fauna are extinct at present.

(2) Cueva de Jiménez, Chihuahua

This cave is 14 km southeast of Jiménez, at 1,450masl. The locality has remains of extinct and extant vertebrates and molluscs. Several rodents are no longer found south of the southern United States. Only two extinct species are known: an undescribed antilocaprid and the rabbit *Aztlanolagus agilis* Russell & Harris, 1986. Neither radiocarbon dating nor stratigraphic controls during excavation have been

undertaken. The fauna is assigned to the Pleistocene/Holocene interface based on its composition.

(3) Cueva de La Boca, Nuevo León

The cave is 3km east of Santiago, at 540masl, in a region with scrubland. The fossil bone is from a tunnel below the main chamber. Among the remains are many reptiles and mammals, including shrews, bats, rodents, and artiodactyls. Most of the identified species are similar to the present regional mammal fauna. The few extinct species like the Pleistocene shrub ox *Euceratherium* sp. allow assigning this fauna to the late Pleistocene.

(4) El Cedral, San Luis Potosí

The site is on "La Amapola" Ranch, El Cedral at 1,700masl. The materials from the excavations are similar to those from Rancho La Brea, California, USA, containing about 40 species, mainly birds and mammals, as well as 20 molluscs species. Radiometric dating indicates a range between 40,000 to 10,500 years before present (BP).



Fig.1- Map with the fossiliferous localities of bat remains in Mesoamerica

TABLE 1. Bat species found in fossiliferous deposits in Mesoamerica (locality numbers correspond to text localities).

SPECIES/LOCALITIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Balantiopteryx io</i>									x								
<i>Peropteryx macrotis</i>														x			
<i>Mormoops megalophylla</i>			x		x		x					x		x			
<i>Pteronotus parnellii</i>													x	x			x
<i>Anoura</i> cf. <i>A. geoffroyi</i>						x											
<i>Artibeus jamaicensis</i>								x	x				x	x	x		
<i>Artibeus lituratus</i>																x	
<i>Carollia subrufa/brevicauda</i>																x	
<i>Centurio senex</i>																x	
<i>Chiroderma villosum</i>														x			
<i>Choeronycteris mexicana</i>					x												
<i>Chrotopterus auritus</i>														x			
<i>Dermanura</i> sp.																x	
<i>Desmodus</i> cf. <i>D. draculae</i>														x		x	
<i>Desmodus rotundus</i>														x			
<i>Desmodus stocki</i>			x		x		x					x					
<i>Diphylla ecaudata</i>														x			
<i>Glossophaga soricina</i>														x			
<i>Leptonycteris curasoae</i>							x										
<i>Leptonycteris nivalis</i>					x				x								
<i>Macrotus californicus</i>							x										
<i>Mimon cozumelae</i>													x				
<i>Sturnira lilium</i>														x			
<i>Sturnira lilium/mordax</i>																x	
<i>Tonatia saurophila</i>																x	
<i>Antrozous pallidus</i>		x															
<i>Corynorhinus townsendii</i>					x												
<i>Eptesicus furinalis</i>													x	x			
<i>Eptesicus fuscus</i>					x												
<i>Lasionycteris</i> cf. <i>L. noctivagans</i>									x								
<i>Lasiurus blossevillii</i>																x	
<i>Lasiurus cinereus</i>					x												
<i>Lasiurus ega</i>														x		x	
<i>Lasiurus intermedius</i>														x			
<i>Myotis californicus</i>					x												
<i>Myotis thysanodes</i>					x												
<i>Myotis velifer</i>			x														
<i>Myotis</i> cf. <i>M. yumanensis</i>									x								
<i>Myotis</i> sp.		x		x			x								x		
<i>Plionycteris trusselli</i>	x										x						
<i>Eumops perotis</i>									x	x							
<i>Nyctinomops aurispinosus</i>									x								
<i>Nyctinomops laticaudatus</i>									x					x			
<i>Tadarida brasiliensis</i>				x					x								
<i>Tadarida</i> sp.		x															
TOTAL	1	3	4	1	9	1	5	1	9	1	1	2	4	15	2	9	1

(5) Cueva de San Josecito, Nuevo León  
San Josecito Cave is southwest from Aramberri, Municipio de Zaragoza, at 2,240masl. Research in the cave has been conducted since the middle 20<sup>th</sup> century. The cave deposits are well-stratified, and some strata have been radiocarbon dated, with a

range of 16,000 to 44,000 years BP. The 120 vertebrate species constitute the most important Pleistocene fauna for México. Recently ARROYO-CABRALES & JOHNSON (2008) documented new findings for the cave mammal fauna, including the additions to the known bat species.



## (6) Cueva de Infiernillo, Tamaulipas

Subfossil bone remains were found in this cave within the Gómez Farías region, including seven bat species (KOOPMAN & MARTIN, 1959). The studied material was associated with a Pleistocene fauna.

## (7) Cueva de La Presita, San Luis Potosí

The locality is 21.4km south of Matehuala, at 1,540masl. The fauna consists of 36 mammal taxa, of which 11 are extinct, including five bat species. This fauna is assigned to the late Pleistocene based on its high proportion of extinct components.

## (8) Gruta de Quintero, Tamaulipas

This cave is located 6km south of Ciudad Mante, at 200masl. The deposit includes some extinct large mammals. Based on these taxa, the fauna is considered to date to the Pleistocene/Holocene interface.

## (9) Cueva de El Abra, Tamaulipas

This cave is near the previous one, within the tropical area of the state, 9km northeast from Antiguo Morelos, at 300masl. An important tropical vertebrate microfauna comes from a travertine layer. The fauna is composed primarily of bats (9 species) and rodents, and is assigned to the late Pleistocene. All of the species are extant, but the extinct mouse *Perognathus huastecensis* Dalquest & Roth, 1970 is known only from this cave.

## (10) Cuencas de Chapala-Zacoalco, Jalisco

Several fossil vertebrates, either complete or incomplete, have been found on the shore line of both Lake Chapala and Lake Zacoalco. Most of those remains are not stratigraphically controlled. During the initial excavations, however, it was possible to identify two distinct Pliocene/Pleistocene and late Pleistocene faunal components.

## (11) Rancho El Ocote, Guanajuato (CARRANZA-CASTAÑEDA &amp; MILLER, 2004; CARRANZA-CASTAÑEDA &amp; WALTON, 1992)

This place is the most important late Hemphillian and Blancan locality in central México, with more than 50 taxa known and several others under study. Another possible bat Hemphillian record was reported for the State of Hidalgo, east from Guanajuato (record not shown in the map).

## (12) Tlapacoya, Estado de México

Tlapacoya Mountain is a small volcanic hill located 26km southeast from downtown México City, at 2,240masl. The known mammal fauna consists

of 22 taxa from a period between 33,150 to 9,000 years BP. The fauna includes both extinct and extant species. Among the extant forms, some still live in the region and others are extralimital.

## (13) Actún Spukil, Yucatán

This large cave is 6km south of Hacienda Calcehtok, at 60masl. A mylodont and other tropical mammal remains have been collected at the deepest portion of the cave. It has been assigned to it a late Pleistocene age.

## (14) Gruta de Loltún, Yucatán

The cave is located 7km south of Oxkutzcab, at 40masl. The vertebrate remains come from archaeological excavations and were assigned to deposits from late Pleistocene and early Holocene. The fauna includes several extinct taxa, like dire wolf, extinct llama, and gomphothere.

## (15) Cueva Encantada de Chimalacatlán, Morelos

The cave is found 2km east of Chimalacatlán, Municipality of Tlaquiltenango, at 1,200masl. The fauna is composed mainly of tropical animals such as ground sloth and gomphothere, but includes extinct temperate taxa, like bison and horses. The fauna is assigned to the late Pleistocene.

## BELIZE

(16) Cebada Cave, Chiquibul System, Cayo District (CZAPLEWSKI *et al.*, 2003)

This cave is part of an extensive cave system formed by 65km of tunnels and chambers. The fauna contains mammals (including human), reptiles, and a young spectacled bear *Tremarctos floridanus* Gidley, 1950; the bear previously was reported from San Josecito Cave. The fauna is assigned to the late Pleistocene or Holocene.

## EL SALVADOR

## (17) Barranca de Sisimico, Department of San Vicente

This open site shows the presence of Neotropical animals that crossed over the Panama Isthmus, including *Megalonyx*, *Eremotherium*, *Mixotoxodon*, *Cuvieronius*, and an extinct cervid. WEBB & PERRIGO (1984) suggested that this fauna needed further study because it might represent the early Pleistocene (Irvingtonian). The bat skeleton comes from diatomaceous deposits below the sandstone; it has not been studied in detail, but it should be since it may represent a new species.

## RESULTS AND DISCUSSION

Currently, records consist of 41 bat species from 17 fossil localities in Mesoamerica: México (15) and Central America (2). Such a number represents 24.8% of the total current species known at the region (165), and includes six out of eight families [Emballonuridae (2 species, 4.9% fossil total), Mormoopidae (2 species, 4.9%), Phyllostomidae (20 species, 48.8%), Antrozoidae (1 species, 2.4%), Vespertilionidae (12 species, 29.3%), and Molossidae (4 species, 9.8%)]. The same families are respectively represented as follows: 11 (6.9%), 5 (3.1%), 72 (45.3%), 2 (1.3%), 47 (29.6%) y 22 (13.8%). Gruta de Loltún is not only the most diverse locality based on bat species found at the fossiliferous deposits in the studied region, but also the place where most abundant remains were collected.

Only one bat species is known at a pre-Pleistocene deposit, being the oldest bat in Mesoamerica. It is *Plionycteris trusselli* Lindsay & Jacobs, 1985, an extinct genus that comes from one locality in northern México (type locality), and two probable occurrences in central México (CARRANZA-CASTAÑEDA & MILLER, 2004); further study of those Central Mexican specimens is needed to corroborate the taxon identity. All other species are from deposits

assigned to the late Pleistocene, and to the Rancholabrean land mammal age (300,000 to 10,500 years BP; Tab.2), although the El Salvadoran specimen may be older. Only two other extinct species come from those deposits, *Desmodus draculae* Morgan, Linares & Ray, 1988 and *D. stocki* Jones, 1958. The other species are extant, and all but two occur at present at the same geographic region where they were found. Two extralimital species, *Balantiopteryx io* Thomas, 1904 and *Eumops perotis* Schinz, 1821, are currently not known from northeastern Mexico where they were found.

Most of the known fossil localities are caves, and only six were open deposits. The same is true for the species' roosting habits, most of them being cave bats, either exclusively or temporally (at least 80%). In regard to food habits, the composition consists of 24 insectivorous bats (57.5%), six frugivorous (15%), five nectarivorous (12.5%), four blood-eaters (10%), and two carnivorous (5%). The piscivorous habit is not represented, but is known for fossil specimens in South America. For the modern bat fauna, food habits follow a different distribution pattern: 108 insectivores (65.5%), 33 frugivores (20%), 15 nectarivores (9.1%), three blood-eaters (1.8%), four carnivores (2.4%), and two piscivores (1.2%).

TABLE 2. Fossil bat localities in Mesoamerica and their absolute or relative age.

LOCALITY	AGE
Yepómera	Late Hemphillian
Cueva de Jiménez	Pleistocene – Holocene
Cueva de La Boca	Rancholabrean
El Cedral	40,000 – 10,500 years BP
Cueva de San Josecito	44,000 – 16,000 years BP
Cueva de Infiernillo	Rancholabrean
Cueva de La Presita	Rancholabrean
Gruta de Quintero	Rancholabrean
Cueva de El Abra	Rancholabrean
Cuencas de Chapala-Zacoalco	Rancholabrean
Rancho El Ocote	Latest Hemphillian
Tlapacoya	33,150 – 9,000 years BP
Actún Spukil	Rancholabrean
Gruta de Loltún	Rancholabrean
Cueva Encantada de Chimalacatlán	Rancholabrean
Cebada Cave	Pleistocene – Holocene
Barranca del Sisímico	Early Pleistocene?

Some of the reasons for the low numbers of fossil bat species known from Mesoamerica are: 1) the lack of detailed collecting methodology for small vertebrates, that has been improved in the recent years by using archaeological excavations methods; 2) the researchers interest in pursuing studies of macrofauna rather than the overall faunal components; and 3) the actual preservation of small mammal remains, that seems more difficult in open spaces than in caves. As for the bat fossil record in Mexico, the presence of three species of the genus *Desmodus* in the Pleistocene is outstanding, as currently only one is extant, *D. rotundus* Geoffroy, 1810. The large size of the extinct species, *D. draculae* and *D. stocki*, may be due to the large-sized animals, like ground sloths and many other megafaunal mammals, on which they fed. These large “mega-vampires,” then, were depleted of their food supply at the time of megafaunal extinction. Small sized species such as *D. rotundus* and *Diphylla ecaudata* Spix, 1823 could survive feeding on smaller herbivorous animals.

#### CONCLUSION

Enhancing the collecting efforts for microvertebrates is critical to gaining a deeper knowledge of the evolutionary pathways for the bats. The same is true for all other microvertebrates. Since caves seemed the best site for fossil bat collecting, the development of cave research protocols for small vertebrate paleontology is needed.

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